Gulf of Mexico Science

Volume 26
Number 2 *Number 2*

Article 3

2008

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DOI: 10.18785/goms.2602.03

Gulf of Mexico Science, 2008(2), pp. 118–123

Social Structure of Sperm Whales in the Northern Gulf of Mexico

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Sperm whales exhibit highly structured social behavior that depends on sex, age, and possibly local ecological characteristics. We analyzed sighting data collected between 1994 and 2005 to determine the social structure of sperm whale groups in the northern Gulf of Mexico (714 good-quality photographs of 285 individual whales). Average typical group size was approximately eight when estimated with mark–recapture techniques and using data from 2003 to 2005. Lagged association rate analyses including data from 1994 to 2004 indicated average group sizes of 11.41. Therefore, groups in the Gulf are considerably smaller than groups in the Pacific Ocean, but similar to those from the Caribbean Sea. Similarly, groups in the Gulf of Mexico remained stable for longer periods (62.5 d, SE = 47.62) than Pacific groups, but were comparable to groups from the Gulf of California. Such differences and similarities between populations could be due to adaptations to local conditions, indicating that Gulf of Mexico sperm whales may live in ecological conditions more similar to those of the Caribbean and the Sea of Cortez than to the Pacific.

Sperm whales (*Physeter macrocephalus*) have been recognized as a social species from earliest whaling days (Melville, 1851; Clark, 1887). Indeed, their social cohesion was used by some whalers to capture as many members of a group as possible. However, our understanding of the structure of sperm whale groups has changed fundamentally in recent years through studies of live animals using techniques such as photo-identification (photo-ID) (Whitehead and Gordon, 1986; Whitehead, 2003). Although whalers perceived groups of sperm whales as male-dominated harems, we now know that the core social units (so-called mixed groups) consist of adult females and their immature offspring, which remain together for years to decades. Large breeding bulls visit these mixed groups only rarely and for brief periods (Whitehead, 1993; Christal et al., 1998). Mixed groups often form larger groupings with one or several other mixed group, staying together for periods of at least several hours (Whitehead, 2003). It is these larger groups that are most commonly encountered in the field. However, while they are foraging, members of these groups typically disperse over several kilometers, so that what a researcher usually encounters in the field are single animals or smaller clusters of whales recovering at the surface between deep dives. (Clusters are defined as animals swimming in a coordinated manner and separated on average by less than a body length [Waters and Whitehead, 1990]). As males mature they leave the mixed groups into which they were born and form all-male groups, which tend to become smaller as the males get older. Morphologically, these maturing males in all-male groups are distinct from mature females by being larger, having proportionally larger heads, and generally lacking dorsal fin calluses (Kasuya and Ohsumi, 1966; Rice, 1989; Clarke and Paliza, 1994). Therefore, they can be reliably recognized as males and distinguished from females in the field.

Here we describe the social behavior of sperm whales in the Gulf of Mexico (GoM) and compare it with data collected from sperm whale populations in the Pacific Ocean and elsewhere using similar techniques. Whitehead (2003) argued that the evolution of the social system of sperm whales was shaped chiefly by life history traits, morphology, ecology, and the interactions of these factors. Thus, comparative information on social organization in different regions may provide a perspective on the ecological constraints for sperm whales in these areas. Knowledge of the social structure of sperm whales in the GoM is also a necessary consideration in management decisions, as, for example, those related to expanding oil and gas exploration and production activities in the deepwater areas of the GoM (Richardson et al., 2004). If managers seek to ensure that current and future anthropogenic activities are managed to minimize their potential impacts, then knowledge of the residency and social structure of the sperm whales frequenting the GoM is an important requirement. Cultural transmission of information between sperm whales (Whitehead, 2003; Whitehead et al., 2004) could include knowledge of, and responses to, anthropogenic activities, resulting in groups of whales that respond differently to such stimuli.

Methods

Photo-ID data were collected in the GoM between 1994 and 2005 during a series of cetacean survey cruises. GulfCet, jointly operated by National Marine Fisheries Service, Southeast Fisheries Science Center (SEFSC) and Texas A&M University (Davis and Fargion, 1996; Davis et al., 2000; Würsig et al., 2000), collected data between 1994 and 1996. SEFSC research projects contributed data over the period between 2001 and 2004 (Mullin and Fulling, 2004, Mullin et al., 2004). The most substantial data set comes from dedicated Sperm Whale Seismic Study (SWSS) cruises, supported by the Minerals Management Service, carried out between 2002 and 2005 (Jochens et al., 2008). Spatial efforts of these projects overlapped completely or to a large extent (Jochens et al., 2008).

In 2002 and 2003, research was carried out from a 60-m oceanographic research vessel (R/V *Gyre*). Sperm whales were detected visually from the flying bridge by observers using stand-mounted "big eye" binoculars (25 × 150 mm), and acoustically, using a towed stereo hydrophone system (Jochens et al., 2008). Once groups of whales had been encountered, small rigid-hulled inflatable boats (RHIBs) were launched to obtain identification photographs (see below) and behavioral observations. RHIBs were able to find and follow submerged whales using directional hydrophones. In 2004 and 2005, surveys were carried out from a 14-m motor sailor (*Summer Breeze*). Sperm whales were encountered mainly by acoustic detection. This smaller vessel did not have a raised observation platform and was much quieter and more maneuverable, so that acoustic detection and tracking was much more efficient than operating from a large vessel. Both photo-ID and behavioral observations were carried out from the sailboat. In all years, groups were followed for as long as possible (subject to weather, logistical constraints, and whale behavior), or until we were confident that all individuals in the group had been photographed for identification.

Sperm whales can be individually identified from photographs showing marks on the trailing edges of their flukes, taken as the whales commence deep feeding dives (Arnbom, 1987). During SWSS field work, we used a Canon EOS 1D camera with a SIGMA 70–300-mm f/4 lens (for equipment details or previous studies, see Davis and Fargion, 1996; Davis et al., 2000; Würsig et al., 2000; Mullin and Fulling, 2004; Mullin et al., 2004). Photographs were scored independently for the extent of marking on the fluke and the quality of the image (defined in terms of its ability to show marks of a particular grade if they were present). Only images capable of showing animals sufficiently marked to allow reliable identification over the time period of this study (Dufault and Whitehead, 1995; Childerhouse and Dawson, 1996) and images of a quality sufficient to reliably show such marks if they were present were included. Using these restrictions, allowed identification of virtually all whales (Dufault and Whitehead, 1995; Childerhouse and Dawson, 1996; Whitehead, 2003) and it is reasonable to assume that the identified whales are representative of the population. Matching of photos was done both visually and using the Phlex matching tool (available from http://homepages.cwi.nl/~adri/europhlukes/flukes/index.html; for a more detailed description of the matching process, see Jochens et al., 2008: section 4.7).

For each group encountered in the field on any particular day, the group size and associated coefficient of variation (CV) were estimated using a Petersen mark–recapture method. Each group was divided into two equal sets, which were used as the two samples for the Peterson procedure (Whitehead, 2003, 2008; Coakes and Whitehead, 2004). Because high-precision estimates of group size are biased against larger groups, and low-precision estimates inflate group size variation, we followed Whitehead's (2003) advice and calculated estimates of group size with high ($CV < 0.25$) and lower ($CV < 0.4$) precision. In order to examine the social structure of the groups we encountered, we calculated the standardized lagged association rate (Whitehead, 1995) using SOCPROG 2.3 (http://myweb.dal.ca/hwhitehe/social.htm). This rate estimates the probability that two animals sighted together at a given point in time are sighted together again after a certain time period (Whitehead, 2008). We also fitted models estimating parameters for group sizes and temporal stability. Five models were tested: constant companions (group members remain in same group permanently), casual acquaintances (individuals associate over short time periods only), a mixture of the two types of groups, and a model that included acquaintances that associate over two different time periods. Parameters in the final model were based on previous research on sperm whale groups in the Pacific (Whitehead, 1995; Coakes and Whitehead, 2004). Model choice was based on the quasi-Akaike information criterion (QAIC) (Whitehead, 2007, 2008). Differences between models in QAIC values (ΔQAIC) of <2 indicate little support for a particular model. Larger differences indicate considerably stronger

TABLE 1. Summary of number of long-term identifications and the proportion of resightings of identified individuals from previous years made during each survey year.

Year	Number of individuals identified	Number of new individuals identified	% Resighting
1994	8	8	–
1996	15	11	26
2000	26	25	4
2001	37	30	19
2002	48	38	21
2003	95	66	30
2004	73	50	31
2005	67	57	14

support for the model with the smallest QAIC value (Burnham and Anderson, 2002).

RESULTS

One thousand and fifty-two identification photographs collected between 1994 and 2004 were available to us for daily group-size analysis. Of these, 714 photos fulfilled our requirements for photographic quality and fluke distinctiveness to be used for long-term identification. Overall, we identified 285 different individuals (Table 1).

Due to different field protocols and available data, only photo-ID data from 2003 to 2005 could be used for group size estimation (Table 2). There were no significant interannual differences in group size (analysis of variance: $F_{2,31} = 0.86$, $P = 0.43$).

A number of lines of evidence indicate that in 2005 the distribution of whales in the northern GoM was different from that in earlier years. For example, relatively few of the mixed groups consistently sighted in the study area in earlier years were encountered. This is reflected in the sharp drop in percentage of resightings in 2005 (Table 1). Maturing males were also seen more frequently in these areas in 2005. Biggs and Jochens (Jochens et al., 2008: section 5.5)

TABLE 3. Parameters for social structure from lagged association rate analyses, with and without 2005 data, based on the custom model including constant companions and short-term acquaintances. Units only comprise the former; groups also include short-term acquaintances. Data on potential males were too few to calculate association rates. ΔQAIC indicates difference in QAIC value to next best model. ΔQAIC values >2 indicate strong support (Burnham and Anderson, 2002).

Parameters	1994–2004 (SE)	1994–2005 (SE)
Unit size	4.76 (3.12)	6.83 (106,873.32)
Group size	11.41 (3.12)	14.95 (1,304.92)
Disassociation rate	0.016 (0.021)	0.006 (1.640)
ΔQAIC	3.33	0.58

provide information on anomalous oceanographic conditions in 2005 that may have contributed to this change in distribution. Because we believed that the data from 2005 might not be representative of the usual situation, we repeated the analysis of lagged association rates without data from that year. Finally, we excluded data from all-male groups; thus, this represents a measure of changes in association between members of mixed groups. The complete analysis showed weak support ($\Delta QAIC < 2$) for the custom model including long-term associates and short-term acquaintances (Table 3). When analyzed without 2005 data, the analysis showed strong support ($\Delta QAIC > 3$) for the same social model (Fig. 1), with an average group size of 11.4 and a rate of associations breaking up (disassociation rate) of 0.016/day (Table 3).

DISCUSSION

Peterson mark–recapture estimates for mixed-group size indicated an average typical group size of approximately eight whales. The comparable estimates for typical group size from the lagged association rate analysis resulted in typical

TABLE 2. Estimated mean group sizes for 2003–05. "Group size" reflects group size as estimated by an observer who is not a member of the group. "Typical group size" estimates adjust for the fact that relatively more individuals are in larger groups (Jarman, 1974) and therefore reflects the group size as experienced by a member of the group. Numbers in parentheses are standard deviations.

	Estimates with CV < 0.25			Estimates with CV < 0.40		
Year	n	Group size	Typical group size	n	Group size	Typical group size
2003	6	5.5 (1.78)	6.0 (1.53)	10	6.9 (4.54)	9.6 (5.97)
2004	10	4.9 (2.84)	6.4 (2.68)	14	5.0 (2.47)	6.1 (2.38)
2005	3	6.5 (7.86)	12.8 (5.40)	7	5.3 (4.84)	9.1 (5.71)
Combined	19	5.2 (3.48)	7.4 (4.03)	31	5.6 (3.78)	8.0 (5.04)

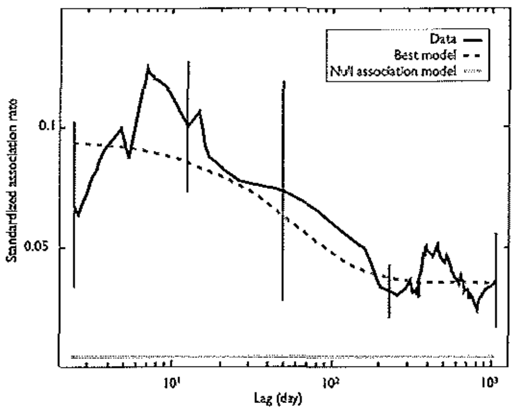

Fig. 1. Standardized lagged association rate for female and immature sperm whales in the Gulf of Mexico, 1994–2004 (blue line). Error bars display ±1 estimated standard error from Jackknife procedure. The best-fitting model was the custom model, shown in green (parameters are provided in Table 3). For comparison, the null association rate (red line) would result from individuals that do not preferentially associate with other whales over any time period.

group sizes of approximately 11 whales. This difference could be caused by the different data sets used for these analyses. The Peterson estimates used data from 2003 to 2005 only, whereas data used for the lagged association rate analysis ranged from 1994 to 2004. Restricting the latter analysis to the same years as the former would have resulted in too few data points for stable modeling.

Both analyses of lagged association rates supported a social model of long-term associates and short-term acquaintances. Excluding the 2005 data in the analysis increased support for this model considerably. This change could be another reflection of the differences that resulted in altered sperm whale distributions and oceanographic conditions described above. Although the currently available data set is too small and short-term to reliably delineate units of animals with long-term associations in the groups we observed (i.e., social units, sensu Whitehead, 2003), it does provide information on the social structure exhibited by sperm whales in the GoM. As in other areas, individual sperm whales in a mixed group share long-term associations with some members of the group, but only associate for short periods with the other members of the group.

Some examples of repeated sightings of animals associated with each other after time periods from weeks to years support this conclusion. For example, two individuals were seen together in 2002, 2003, and 2004; a third animal was observed with them during 2003 and 2004. Another two whales were identified together in 2000, 2003, and 2004, with a third animal joining them in 2003 and 2004.

Typical group sizes in the GoM of about eight individuals were considerably smaller than those reported from waters off Chile or the Galápagos Islands, where group sizes range between 24 and 31 individuals (Coakes and Whitehead, 2004), but similar to the average group size of approximately six reported from the Caribbean (Gero, 2005) (all estimated with Peterson mark–recapture techniques). GoM sperm whales also differ in other characteristics from those studied in the Pacific. For example, sperm whales in the GoM are significantly smaller in size than those in other areas (Jaquet, 2006). Such population-wide differences could reflect different environmental conditions, ecological adaptations, or population dynamics. For example, smaller groups and smaller individuals may be better adapted to an environment in which prey is less abundant (Baird and Dill, 1996; Connor, 2000). However, our data set from the GoM is still small compared to those from other areas, and given the large interannual variability we observed, it remains to be seen how well our estimates approximate long-term values.

Analysis of lagged association rate indicated a disassociation rate of 0.016 in the GoM, which corresponds to groups remaining stable for 62.5 d (SE = 47.62 d). This is considerably longer than in the Pacific, where groups stayed together for between 7.5 and 19 d (Coakes and Whitehead, 2004). However, sperm whale groups in the Sea of Cortez also remained stable for longer periods (approximately 80 d) (Jaquet et al., 2005). Whitehead (2003) hypothesizes that differences in ecological characteristics, such as predation pressure and food availability, may determine the social organization of sperm whales. Given our current results, sperm whales in the GoM may live under ecological conditions more similar to those in the Sea of Cortez than to those of the Pacific. However, a larger and more long-term data set on sperm whale social systems is required to confirm our available results from the GoM. As pointed out by Jaquet et al. (2005), this should be a priority of future research. Information on predator distributions and food availability is also necessary.

This information is also important from a management perspective because cultural transmission of information between sperm whales (Whitehead, 2003; Whitehead et al., 2004) could include knowledge of and responses to anthropogenic activities, resulting in groups of whales that respond differently to such stimuli. In turn,

DOI: 10.18785/goms.2602.03

this would imply that activities have to be managed accordingly. Irrespective of whether whales are already impacted by current anthropogenic activities, the population and its environment should be monitored regularly to enable early detection of population changes and link them to possible causes.

Acknowledgments

This study was funded by the Minerals Management Service under Cooperative Agreement 1435-01-02-CA-85186. This work would not have been possible without the dedication and hard work of all observers and crews on the R/V *Gyre* and the *Summer Breeze*. The support of Bill Lang and Ann Jochens at Minerals Management Service was instrumental throughout all phases of the project. We also thank Stacie Arms of Texas A&M at Galveston for her untiring efforts. Keith D. Mullin helped with photo-IDs from previous research projects. Ricardo Antunes, Luke Rendell, and Hal Whitehead provided crucial help during analysis. Two anonymous reviewers and Keith D. Mullin provided valuable suggestions for improvements.

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DOI: 10.18785/goms.2602.03